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Leiden
The Netherlands

Sexual selection and speciation: mechanisms in Lake Victoria cichlid fish

Maan, M.E.

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Chapter 9

‘The males sedulously court the females, and (...) take pains in displaying their beauty before them. Can it be believed that they would thus act to no purpose during their courtship? And this would be the case, unless the females exert some choice and select those males which please or excite them most. If the female exerts such choice, all the above facts on the ornamentation of the males become at once intelligible by the aid of sexual selection.’

Darwin, 1871 (on sexual selection in fishes)



Synthesis

In this final chapter, I summarise the main findings of the work presented in this thesis. I discuss their implications for our understanding of haplochromine speciation, and I briefly indicate how my results may affect the direction of future work.

Sexual selection within species as the basis for divergence?

Previous studies of haplochromine species diversity (Albertson et al. 1999; Knight 1999; Seehausen 1999) have provided support for the hypothesis that sexual selection on male nuptial coloration can drive haplochromine speciation. As a possible mechanism, Seehausen et al. (1997a) suggested that colour morphs or variants of the same species may become reproductively isolated due to divergent sexual selection. In this thesis, I have investigated several components of this mechanism in two genera of Lake Victoria haplochromines.

Firstly, the proposed mechanism entails that male nuptial coloration is subject not only to selection exerted by inter-specific mate choice, but also to intraspecific directional sexual selection (Lande 1981; West-Eberhard 1983; Boake 2002). In the closely related species pair *Pundamilia pundamilia* and *Pundamilia nyererei*, Seehausen & van Alphen (1998) had already demonstrated the former: females use male coloration as a cue in interspecific mate choice. As described in Chapter 2 of this thesis, I found that *P. nyererei* male nuptial coloration is subject to intraspecific directional sexual selection by female choice, thereby confirming the second prerequisite of the proposed mechanism for one of the two species. Future work should establish whether the same holds for *P. pundamilia*; the findings presented in Chapter 4 suggest that also in *P. pundamilia*, females may prefer to mate with the most conspicuously coloured males (see below).

Secondly, in the mechanism outlined above, the starting point for species divergence is provided by intraspecific colour variation that is genetically determined. In *Pundamilia*, heritability of male nuptial coloration has been established by laboratory breeding, both for the two reproductively isolated species, as well as for hybridising populations (Seehausen et al. 1997a; I. van der Sluijs pers. comm.; pers. obs.). In this thesis, I investigated another example of colour variation: the apparently continuous variation from yellow to blue in both sexes of *Neochromis omnicaeruleus*. In Chapter 7, I demonstrated that in this species, besides developmental and environmental factors, individual coloration is related to the colour of the parents. Hence, the studied population harbours genetic variation for coloration and/or the process of colour change. Since blue-red and blue-yellow colour polymorphisms and species pairs are common among Lake Victoria haplochromines (Seehausen et al. 1999c), these findings provide support for the hypothesis that species divergence could start from intraspecific colour variation. In the case of *N. omnicaeruleus*, the mechanism of ontogenetic colour change and its potential to respond to natural or sexual selection remains to be investigated. For

example, artificial selection in the laboratory may produce separate blue and yellow populations. Further, laboratory experiments could investigate the presence of colour-based mating preferences, and the physiological mechanisms and environmental factors that determine colour development.

The third major component of the speciation mechanism is a source of divergent selection on coloration and/or on colour preferences. In Chapter 5, I presented evidence to indicate that a heterogeneous light environment may exert divergent natural selection on visual properties and on male nuptial coloration. I found that females of *P. pundamilia* and *P. nyererei* differ in their behavioural responses to blue and red light, in a way that matches the difference in the hue of male nuptial coloration between the species. I proposed that the spectral depth gradient in the Lake Victoria waters entails that individuals with increased red-sensitivity, communicating by use of red signals, are at an advantage in deeper water, whereas individuals with increased blue-sensitivity, using blue signals, do better in shallow water. Several studies have identified genetic variation for colour perception in haplochromine cichlids (Carleton & Kocher 2001; Terai et al. 2002), including *P. pundamilia* and *P. nyererei* (Carleton et al. 2005). The experiment described in Chapter 5 is the first study that demonstrates interspecific differences in colour perception at the behavioural level, in a pair of very closely related species. Together with female preferences for conspicuously coloured males, as demonstrated for *P. nyererei* in Chapter 2, this divergent natural selection on visual properties provides a mechanism for population divergence.

It must be noted however that none of the studies mentioned above, including mine, have established a direct relationship between female colour perception (quantified as optomotor response thresholds, or inferred from opsin gene sequences or protein structure) and female mating preferences for male nuptial coloration. To assess the potential of divergent sensory drive as a mechanism of speciation, this relationship must be tested. This can be done by measuring both visual sensitivity and mating preferences in the same sample of individuals, preferably including interspecific hybrids. Artificial selection in the laboratory may provide additional support, when colour sensitivity and colour preference show a correlated response to selection. In guppies, selection lines with increased sensitivities to certain colours have been established (Endler et al. 2001), indicating that this approach may be fruitful also in cichlids. The considerably longer generation times in cichlids however will make that such experiments require several years.

The costs of bright colours: parasites and predators

Female preference for conspicuous males can evolve in many different ways, and several mechanisms may operate simultaneously (Andersson 1994). Females may simply mate with the first male they detect in order to minimise search costs. This strategy may be beneficial when potential mates are scarcely distributed or difficult to detect (e.g. in turbid water). As discussed in Chapter 5 (see above), female preferences for conspicuous colours can evolve as a by-product of the evolution of sen-

sory properties ('sensory bias', e.g. Ryan 1990; Endler 1992). When conspicuous signals are costly to produce or maintain, female choice for those signals may be driven by handicap selection: handicapping ornaments can only be afforded by individuals of sufficient quality (Zahavi 1975). Colours can be costly in several ways. They may require resources that would otherwise be available for other physiological processes, such as immune defence (Chapters 3 and 4). Further, bright colours may increase an individual's conspicuousness not only to choosy females, but also to predators (Chapter 8).

1) Parasite-mediated sexual selection

In both *P. pundamilia* and *P. nyererei*, I found that male nuptial coloration was related to infestation with macroparasites, with high colour scores correlating with low parasite loads (Chapters 3 and 4). In *P. nyererei*, the relationship between male red coloration and parasite resistance was recently confirmed in a laboratory study involving experimental infection of males of the same population (Dijkstra, Hekman, Schulz & Groothuis in prep.). Thus, in *P. nyererei*, the evidence suggests that carotenoids may mediate a trade-off between sexual signalling and immune defence, making male red coloration an honest signal of individual quality. For *P. pundamilia* however, the evidence is not as strong: my sample sizes were small and statistical power was limited. Moreover, the physiological mechanism underlying the relationship between blue coloration and immune defence remains unclear. Whereas in *P. nyererei* the trade-off between male nuptial coloration and parasite resistance may be mediated by carotenoids (Lozano 1994; Olson & Owens 1998), the blue coloration of *P. pundamilia* is carotenoid-independent. Further, as noted above, it is unknown whether female *P. pundamilia* exert directional sexual selection on the blue coloration of *P. pundamilia* males. Whereas Seehausen & van Alphen (1998) demonstrated that *P. pundamilia* females prefer conspecific males over *P. nyererei* males, and that they use male colour as a cue, we do not know which male traits determine intraspecific mate choice in *P. pundamilia*. Given the relationship with male parasite load (Chapter 4), we may expect *P. pundamilia* females to exert directional selection on male blue coloration. However, as is the case in *P. nyererei* (Chapter 2), *P. pundamilia* female preferences may be influenced by other male characteristics too, such as male size and display activity, territory size and quality, and other aspects of male coloration. In particular, the red coloration in the anal, caudal and dorsal fins of male *P. pundamilia* may affect female choice. This red coloration is not fully expressed until males are sexually mature, suggesting that it may play a role in sexual selection. Despite its carotenoid content however, the amount of red fin coloration was not related to parasite load. Possibly, it is intra- rather than intersexual selection that acts on these red fins: they may for example play a role in male-male competition for territories.

P. pundamilia and *P. nyererei* showed highly significant differences in the infestation rates of several parasite species, consistent with the ecological differences between the species. This indicates that *P. pundamilia* and *P. nyererei* differ in parasite exposure and/or resistance, and that they are subject to different selective re-

gimes in this respect. If trade-offs exist between resistance to the different parasite communities, niche differentiation could cause divergent selection due to differences in parasite exposure. Currently, there is no evidence for such trade-offs. However, given the habitat-dependent conspicuousness of male nuptial coloration, parasite-mediated sexual selection for conspicuous colours may contribute to the maintenance of reproductive isolation between the two species. This indicates that in a heterogeneous environment, good-genes sexual selection does not necessarily preclude species divergence by sexual selection. These findings are in line with recent theoretical studies which show that female preferences for locally adapted males may drive speciation (Edelaar et al. 2004; Reinhold 2004). Moreover, when fitness benefits accrued from female preferences are affected by both signal detectability and information content, they can be maximised in more than one preference-trait combination, especially in heterogeneous environments (Schluter & Price 1993).

Future work should address the heritability of parasite resistance. First, it should be tested whether female choice for bright red or bright blue males improves the parasite resistance of their offspring (e.g. Barber et al. 2001). Second, if parasite-mediated sexual selection is indeed divergent between the two species due to trade-offs in resistance, it follows that each species performs better in its own habitat than in the habitat of the other species, and that hybrids are at a disadvantage in both parental niches (Schluter 2001). Whereas experimental tests of this prediction may not be feasible, experimental infection in the laboratory could provide evidence for this hypothesis: trade-offs and hence divergent selection would be implicated when intraspecific hybrids have lower resistance than either parental species. Third, it may be worthwhile to study the relationships between male coloration and parasite load in populations with different levels of gene flow between *P. pundamilia* and *P. nyererei*: in turbid water populations, where the two species' niches overlap (see below), parasite-mediated divergent selection may be weak.

Finally, it must be noted that parasite resistance is only one of possibly many aspects of individual quality that females may assess during mate choice. My findings that female *P. nyererei* mate multiply, and that male coloration is not related to territory size or body size (Chapters 2 and 3), suggests that male fitness is a complex trait that cannot be assessed perfectly from just one or two characters. Therefore, to understand the evolutionary consequences of female selectivity, it would be important to further investigate the organisation of female mate choice decisions: how many males do females sample, is there variation among and within individual females, and do consecutive sires increase in assessed quality (e.g. Pitcher et al. 2003)?

2) Predation

Conspicuous colours and ornaments may increase the risk of predation. As a result, brightly coloured individuals that survive despite this disadvantage, will tend to possess compensatory survival abilities - they may be particularly good swim-

mers, or they manage to defend high-quality territories, or perhaps they are more vigilant than other individuals. According to the handicap principle, female choice evolves to provide the offspring with these qualities, yielding mating preferences for conspicuously ornamented males (e.g. Rosenthal et al. 2001; Godin & McDonough 2003).

In this thesis, I have not directly addressed this hypothesis, but my findings do support the idea that predator-mediated handicap selection may play a role in haplochromine colour evolution. In Chapter 8, I investigated whether differential predation with regard to colour and sex may contribute to the maintenance of a blotch colour polymorphism in *Neochromis omnicaeruleus*. I demonstrated experimentally that the blotched morphs may incur increased predation risk from visually hunting bird predators. Since sex-linked blotch polymorphisms occur in many cichlid species (Lande et al. 2001), differential predation may play a role in other species too. Moreover, I found that the orange-blotched fish in particular were attractive for the pied kingfishers, a result that may be extrapolated even further. For example, the bright red and yellow *P. nyererei* males may be very attractive to predators as well. Unfortunately, experiments using *P. nyererei* were unsuccessful: males do not develop their bright colours until they have reached a size that cannot be handled by pied kingfishers. To test the hypothesis that *P. nyererei* coloration is a handicap in terms of predation risk, other experimental designs are required. One could use aquarium-raised offspring from wildcaught fish, because these reach sexual maturity (including full expression of nuptial coloration) at a size that will be accepted by pied kingfishers. Alternatively, other predatory species can be used. Cormorants and otters for example are large enough to handle adult *P. nyererei* males. Moreover, in nature, these species are more important predators for *P. nyererei* than are pied kingfishers. Cormorants have been successfully used in predation experiments with sticklebacks (Vamosi 2002).

The results described in Chapter 8 present the first experimental evidence that the conspicuous colours of cichlid fish are costly in terms of increased predation. However, this Chapter aimed to test a more specific hypothesis: that the phenotype frequencies of *N. omnicaeruleus* in nature, which are inconsistent with expectations derived from laboratory crosses, could be explained by differential predation on blotched males (Seehausen et al. 1999b). Consistent with this hypothesis, I found that the blotched colour patterns (the orange-blotched pattern in particular) attracted more bird attacks, and that territorial defence and courtship behaviour would expose males more than females. However, the finding that blotched males were rare already as juveniles, suggests that either they are only rarely produced, or that they experience higher mortality at pre-reproductive age, rather than suffering from increased predation as sexually mature territorial males. Thus, whereas my study identifies differential predation as an important selection pressure, it does not suffice to explain the skewed distribution of blotched phenotypes among males and females in this species in nature. Probably, the underlying genetics of male rescue and blotch expression are more complicated than laboratory crosses suggested (Seehausen et al. 1999b). Additional ge-

netic factors may be identified in large-scale crossing schemes. Further, field observations on mating behaviour of different morphs and of both sexes will be required to distinguish genetic and environmental determinants of phenotype frequencies in nature.

Environmental constraints: the role of the ambient light spectrum

The low transparency of the Lake Victoria waters creates an underwater light environment that rapidly changes with depth. Moreover, water transparency varies considerably between different parts of the lake. This variation in ambient light spectrum is an important selection pressure in the evolution and maintenance of haplochromine colour diversity. In several Chapters of this thesis therefore, the role of the ambient light spectrum was explicitly addressed.

1) Intraspecific sexual selection along a transparency gradient

Seehausen et al. (1997a) showed that the rate of hybridisation between *P. pundamilia* and *P. nyererei* increases with decreasing water transparency, and that the saturation of *P. nyererei* red nuptial coloration is lower in turbid water populations. The authors proposed that turbid water precludes visual mate choice, resulting in relaxation of sexual selection on male coloration.

In Chapter 6 of this thesis, I investigated the mechanism underlying the correlation between male colour and water turbidity, comparing two populations from islands that differ considerably in water transparency. I showed that the two populations do not only differ in the amount and hue of male red coloration, but also in female mate choice behaviour, with females from turbid water being less choosy with regard to male red coloration. This indicates that male coloration and female choice co-evolve in response to variation in water transparency. The alternative hypothesis, that weaker female preferences are the result rather than cause of introgression of *P. pundamilia* genes, seems unlikely. This is because the variation in *Pundamilia* male nuptial coloration in this population is clearly clustered in two distinct phenotypic classes, blue and red. Moreover, female preferences for these male types are probably fully divergent too. Species-assortative mating preferences have not been studied in this population, but females of the comparable population of Python Island show strong and consistent species-assortative mating preferences (Seehausen & Van Alphen 1998; Haesler & Seehausen 2005). These observations argue against strong admixture of species-specific genes for mating preferences and mating traits between *P. pundamilia* and *P. nyererei*.

I also found that in the turbid waters of Kissenda Island, *P. nyererei* inhabits a shallower habitat than at Makobe Island where water transparency is relatively high. These population differences in depth distribution and in the hue of male coloration are consistent with general trends that exist across five populations of *P. nyererei* in the south-eastern part of the lake (Figure 9.1).

With increasing turbidity, *P. nyererei* moves to shallower habitats and the hue of male red coloration tends to become more orange. These changes are likely adaptations to the ambient light spectrum: in turbid water, light intensity decreases more rapidly with depth than in clear water, hampering visual detection of food, predators and potential mates. We now have evidence for three different mechanisms by which *P. nyererei* responds to this selection pressure. Firstly, *P. nyererei* moves to a more shallow habitat. This niche shift may have ecological consequences in terms of diet and competition with other species: increased water turbidity may reduce ecological niche space and increase competition for food and space in shallow habitats. The association between water transparency and depth distribution may apply more generally for Lake Victoria haplochromines, constituting a potential threat to local species diversity. A second adaptation was recently demonstrated by Carleton et al. (2005): in the turbid-water population from Python Island, both *P. nyererei* and *P. pundamilia* were found to have higher proportions of long wavelength-sensitive cones than those from the clear-water Makobe population. As such, the wavelength sensitivities of the fish correspond better

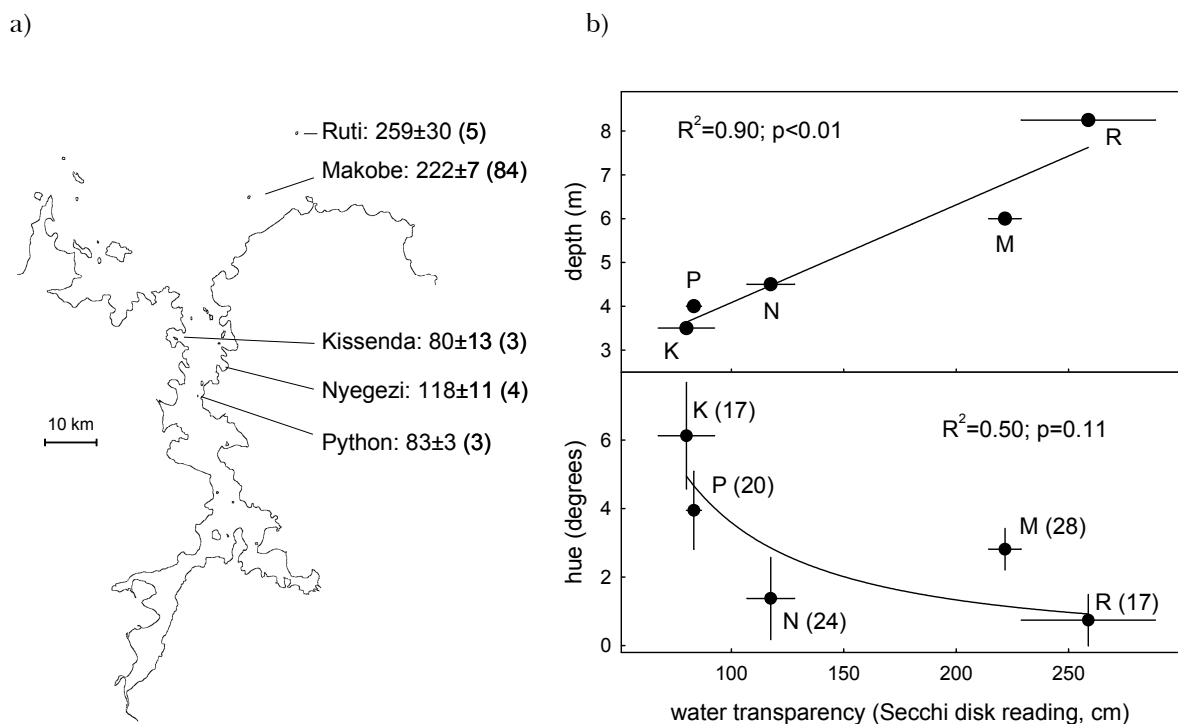


Figure 9.1 Five populations of *P. nyererei* at locations with different water transparencies. a) The Mwanza Gulf and western Speke Gulf with population locations and their water transparencies (mean and standard error of Secchi readings, with the number of measurements in brackets). b) Upper panel: the depth of maximum *P. nyererei* abundance, estimated from angling and gillnetting catches, and from underwater observations (for Ruti and Makobe Islands). Lower panel: the hue of male red coloration, measured in degrees on a standard colour wheel. Sample sizes are given in brackets. Locations: K=Kissenda Island; P: Python Island; N: Nyegezi; M: Makobe Island; R: Ruti Island. Data were collected in 2001-2003.

to the red-shifted ambient spectrum in more turbid water. Finally, I found that males from more turbid water had lower redscores and that females showed an associated decrease in selectivity with respect to this trait. Further work should establish whether female mate preferences in other populations follow the same tendency. Moreover, while the hue of male red coloration changed in a direction that is likely to enhance conspicuousness to females, my experiments did not test female preferences for male hue. Therefore, the hypothesis that a decrease in water transparency coincides with a shift in female preference for more orange-ish male coloration, remains to be tested.

As discussed in Chapter 6, the association between water transparency and sexual signalling also affects the information content of the male signal. Turbid waters may enable *P. nyererei* males to attract females with carotenoid-poor, relatively 'cheap' coloration that does not reliably predict male quality. This mechanism would provide an alternative explanation for a decrease in female selectivity with regard to male red coloration. Quantitative analysis of carotenoid availability and parasite infestation rates in different populations are required to investigate this hypothesis (e.g. Grether et al. 2005). Finally, in Chapter 4 I proposed that divergent sexual selection for parasite resistance contributes to the maintenance of reproductive isolation between *P. pundamilia* and *P. nyererei*. If, in turbid water, depth segregation is absent and male coloration does not reliably indicate quality, divergent selection may be weak. In these environments, reproductive isolation may not evolve. These ancestral *Pundamilia* populations are likely to resemble those present in initially clearer waters that have recently become turbid due to eutrophication. In these populations, secondary hybridisation may have caused mixture of *P. pundamilia* and *P. nyererei* genes into one hybrid gene pool. Molecular genetic tools may provide the means to distinguish between these alternatives for the *Pundamilia* populations in the southern Mwanza Gulf.

2) Water turbidity and visual predation

Visual predators are expected to spot conspicuous prey most easily in clear water (Cezilly 1992; Moyaho et al. 2004) and in the Mwanza Gulf, piscivorous birds tend to be more numerous on clear-water shores (Seehausen et al. 1997a; pers. obs.). Paradoxically, brightly coloured haplochromines, including the blotched phenotypes of several species, are most abundant in clear water (Seehausen & Bouton 1996; Chapter 6).

Conspicuousness is determined by a variety of factors, including the intensity and hue of the colour pattern, the background against which it is observed, the visual properties of the observer, and the intensity and spectral composition of the ambient light (Endler 1978). I cannot rule out the possibility that the blotched colour pattern of *N. omnicaeruleus* has a disruptive or camouflaging effect (Greenwood 1956; Snoeks 1994), especially in clear, shallow water, where sunlight produces irregular patterns of light and dark on the rocks. However, whereas this effect would explain the absence of blotched fish in turbid water, it would also lead

to decreasing numbers of blotched fish with increasing water depth. At Makobe Island, there was a significant trend in the opposite direction (Chapter 8).

As yet another explanation, the difference in conspicuousness between plain and blotched phenotypes may be smaller in clear than in turbid water. This is because the visibility of the plain fish may decrease faster with increasing turbidity than the visibility of the blotched fish. However, this hypothesis is inconsistent with the results of the predation experiment (Chapter 8): predation risk for blotched fish was much higher than for plain fish, although the experimental pond contained clear water and all fish were visible from above. This indicates that the difference in predation risk between plain and blotched morphs is not a direct function of water transparency.

Despite providing evidence for differential predation with regard to colour pattern, I conclude that my results suggest that the effects of sexual selection outweigh those of differential predation. Sexual selection on visual cues is likely to be stronger in clear water (Seehausen et al. 1997a; Järvenpää & Lindström 2004; Chapter 6). For example, the persistence of bright red *P. nyererei* at Makobe Island suggests that predation pressure is strongly opposed by sexual selection by female mate choice. Cormorants and otters were repeatedly seen in the *P. nyererei* habitat at Makobe, and we once observed a cormorant on the surface with a large *Pundamilia* ‘pink anal’ male in its beak. This species breeds sympatrically with *P. nyererei*. Nevertheless, among the territorial *P. nyererei* males that I observed there ($n=28$; Chapter 2), none disappeared during the five-week study period. The available evidence therefore suggests that, in providing an explanation for the evolution and persistence of haplochromine colour patterns along a turbidity gradient, the effects of visual predation are outweighed by the increased potential for visual mate choice in clear waters.

3) Species divergence along a spectral gradient

Besides geographical variation in turbidity between sites, the high organic content of the Lake Victoria waters creates habitat heterogeneity in light regime within sites: short wavelengths are selectively absorbed and scattered from the downwelling spectrum, resulting in a more red-shifted spectrum towards deeper water (De Beer 1989; Chapters 5 and 6). As a result, maximum conspicuousness of male nuptial coloration is achieved in different ways at different depths. Fish spectral sensitivities tend to match the ambient spectrum of the environment, in haplochromine cichlids (Van der Meer & Bowmaker 1995; Carleton & Kocher 2001; Carleton et al. 2005) as well as in other fish species (Loew & Lythgoe 1978; Bowmaker 1995; Cummings & Partridge 2001; Jokela et al. 2003). Therefore, female choice for conspicuous males may select for different male colours at different water depths. Together, these processes constitute divergent selection on male nuptial coloration and a possible mechanism for rapid speciation (Seehausen et al. 1997a; Carleton et al. 2005; Chapter 5).

The importance of inter- and intraspecific variation in visual properties for cichlid speciation is increasingly acknowledged (Sugawara et al. 2002; Terai et al.

2002; Spady et al. 2005). However, correspondence between differences in wave-length sensitivity, male nuptial coloration, female mating preferences and ambient light spectrum between sister species has now been established for only one species pair: *P. pundamilia* and *P. nyererei*. The generality of these findings is yet to be determined. In *N. omnicaeruleus* for example, I did not find any evidence for depth segregation between the blue and yellow colour morphs (Chapter 7). The distribution of differently coloured morphs or species is affected by several other selection pressures, such as predation, parasite exposure and dietary requirements. Moreover, recent studies indicate that male-male competition may be an important determinant of coexistence and spatial distribution of colour morphs and closely related species (Mikami et al. 2004; Seehausen & Schluter 2004; Dijkstra et al. 2005). Future work should establish the relative importance of these selection pressures and their interactions in speciation and species coexistence of haplochromine cichlids.

Conclusions

In this thesis, I have presented evidence for several selection pressures that co-determine colour evolution and population divergence in haplochromine cichlids. My results provide evidence that in *Pundamilia*, female choice for brightly coloured males (Chapter 2) may be driven by ‘good genes’ selection: brightly coloured males have lower parasite infestation rates (Chapters 3 and 4). Further, I have shown that species differences in female preferences for male colours coincide with species differences in visual sensitivities, indicating that mating preferences may evolve as a by-product of natural selection for increased visual performance (Chapter 5). Photic habitat heterogeneity provides the mechanism by which sexual selection through sensory drive becomes an agent of diversification. If the differences in parasite infestation rates between *P. pundamilia* and *P. nyererei* are due to differences in resistance rather than differences in exposure alone, and if there are trade-offs between the resistance to different parasites, female choice for resistant males could contribute further to the maintenance of reproductive isolation between these species (Chapter 4). By extrapolation (Chapter 8), I propose that *P. nyererei* nuptial coloration can be considered a ‘handicap’ in terms of predation pressure. Finally, variation in water transparency among *P. nyererei* populations has a profound influence on visual signalling between the sexes, with both female preferences and male colours changing with the signal propagation properties of the environment (Chapter 6).

In *Neochromis omnicaeruleus*, I showed that the colour variation that exists among the so-called ‘plain’ morph is determined by both genetic and environmental factors (Chapter 7). Pending further study, I suggest that this kind of intraspecific colour variability may provide a starting point for species divergence. In Chapter 8, I provided the first experimental evidence for differential predation on haplochromine colour patterns: blotched morphs of *N. omnicaeruleus* attract more predator attacks. Albeit insufficient to explain the skewed distribution of phenotypes in nature, my results indicate that differential predation with regard

to colour and possibly sex, is a selection pressure that must be taken into account in studies of haplochromine colour evolution.

My work has shown that the evolution of haplochromine colour patterns is subject to several simultaneous selection pressures. In particular, I have demonstrated that the interaction between sexual selection and habitat heterogeneity, in terms of photic environment and parasite exposure, may promote population divergence in male nuptial coloration and female preferences. In contrast, predation pressure and water turbidity may constrain the evolution and persistence of conspicuously coloured morphs and species.

Effective nature conservation requires insight in the biological processes that underlie the evolution and maintenance of biodiversity. Therefore, whereas my work primarily addressed fundamental questions about the mechanisms of haplochromine speciation, I hope that my results will eventually contribute to successful conservation of the Lake Victoria ecosystem.